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Effect of native habitat on the cooling ability of six nursery-grown tree species and cultivars for future roadside plantings

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ABSTRACT

Vegetation in urban areas provides benefits to people, which are increasingly assessed and valued as ecosystem services (ESS). The regulation of the urban microclimate is one of these services, since trees have the potential to reduce urban heat loads by evapotranspiration and shading. Simultaneously, it has been suggested that trees from dry habitats should be used to cope with the increasing risks of drought under climate change in Central Europe. The underlying properties that enable those trees to reduce dependence on the environment, however, are assumed to come at the expense of biomass production and water loss. In the potentially conflicted area between drought tolerance and ESS we compared water consumption, water-use efficiency (WUE), crown structure and growth of six roadside species/cultivars, which are assumed to vary in drought tolerance, due to differing resource supplies in their native habitats. *Acer platanoides, Carpinus betulus* 'Fastigiata', and *Tilia cordata* 'Greenspire' were compared with *Acer campestre*, *Ostrya carpinifolia,* and *Tilia tomentosa* 'Brabant', the latter presumably being less water-demanding. Measurements took place in the municipal nursery of Munich during summer 2016.

Surprisingly, the less water-demanding species/cultivars exhibited on average 1.24 times higher values of maximum daily sap flux density and up to seven times higher growth rates, both contributing to higher WUE. Scaled to leaf level, however, their mean daily transpiration rates were on average lower (0.21 and 0.31 kg H_2O m^{-2} d^{-1}, respectively). They also showed higher flexibility in response to changing weather with increased growth and transpiration under favorable conditions in early summer, but a more conservative water use in dry late summer. The results suggest that these species/cultivars tend to regulate their water use stronger under increasing dryness, whereas canopy size and leaf amount are still the main important determinants of species and cultivar differences in water use.

1. Introduction

Vegetation in urban areas provides benefits to people, which are increasingly assessed and valued as ecosystem services (ESS). Urban trees are considered to be of particular relevance in this context due to various factors, including their ability to absorb and store carbon (Nowak et al., 2013), remove air pollutants (Nowak et al., 2006) and retain and infiltrate stormwater (Xiao et al., 2000a,b; Armson, 2012). Their capacity to moderate urban climates and adapt cities to the adverse effects of climate change has received particular attention recently (Zölch et al., 2016; Rahman et al., 2017).

Urban trees are known to reduce urban heat loads by evapotranspiration and shading (Armson, 2012; Gillner et al., 2015b). Dense tree canopies can reflect and absorb a large share of the incoming solar radiation so that surface temperatures under tree shade can be reduced by up to 19 °C (Armson et al., 2012). The magnitude of thermal comfort within and below the crown depends on tree height, crown density, size and shape (Armson, 2012; Armson et al., 2012; Gillner et al., 2015b; Rahman et al., 2015). Gillner et al. (2015b), for instance, measured common tree species and cultivars in Dresden, east Germany, and found that one unit increase in leaf-area density (m^2 m^{-3}; LAD) can reduce surface temperatures of asphalted streets by 4.63 °C on hot cloudless summer days.

Furthermore, there are significant correlations between transpiration rates of trees and their rate of cooling of the surrounding air (Gillner et al., 2015b; Rahman et al., 2017). Rahman et al. (2017) found

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a temperature reduction of up to 3.5 °C within the crown radius of adult *Tilia cordata* trees during hot summer days in street canyons of Munich, south Germany. The term 'transpirational cooling', however, may lead to confusion since it is not cooling as such, but rather 'warming less' (Kiermeier, 1995); incoming energy is used to convert water into water vapor rather than being transferred to sensible heat. The degree of water loss via transpiration namely depends on the amount of the transpiring surface (Lösch, 2003; Peters et al., 2010), which influences both the within and the below-crown microclimate.

Results from several studies have shown that the magnitude and seasonality of the microclimatic benefits of trees strongly depend on species (Leuzinger et al., 2010; Armson, 2012; Rahman et al., 2015) or rather plant functional types (Peters et al., 2010), growing conditions (Ferrini and Baietto, 2006; Armson, 2012; Rahman et al., 2017), management (Ferrini and Baietto, 2006), and planting design (Armson, 2012; Norton et al., 2015). Therefore, informed selection and strategic placement of urban trees as key elements of the urban green infrastructure (Pauleit et al., 2011; Zölch et al., 2016) are crucial for achieving the greatest microclimatic impact. However, there is still a gap of knowledge concerning the relative effectiveness of different urban tree species and particularly cultivars (Armson, 2012; Roloff, 2013; Rahman et al., 2015).

At roadsides with their high evaporative demands, impervious surfaces, de-icing salts, and re-radiation effects, growth conditions of urban trees are most extreme and the impacts of climate change likely to be particularly severe; increased signs of drought stress show that tree species/cultivars that have evolved in Central European woodlands under a temperate climate regime do not cope very well with increasingly harsh urban growth conditions (Roloff, 2013). This has led researchers to look for alternative (non-native) tree species and cultivars, which are assumed to be better adapted to heat, drought, and pests (Duhme and Pauleit, 2000; BdB, 2008; Sjöman et al., 2012). Several ongoing field studies have been rating species and cultivars from drier habitats for their suitability for future plantings (e.g., GALK, 2006 & 2012; Fini et al., 2009; Hiemstra, 2011; LWG, 2016). Additionally, assessments have been attempted on the basis of knowledge about the environmental conditions in the natural habitats of species (BdB, 2008; McCarthy et al., 2011). The basic premise of all these approaches is that the respective resource supply in the native habitats affects the environmental tolerance of the investigated tree species/cultivars. Plants that are exposed to limited availabilities of resources are considered to display some specific structural and functional adjustments and response capacity to overcome stress conditions.

Some of these adaptions, however, are assumed to reduce photosynthesis and growth concurrently with water consumption (Chapin et al., 1993; Lösch, 2003). This causal relationship is driven by the inherent link between water loss and carbon gain: if stomatal conductance (g_S) is lowered to avoid tissue water deficits under stressed conditions, the influx of CO_2 into the leaves is also reduced. On the other hand, species found in areas with low water availability also tend to have greater water-use efficiency (WUE) at leaf and tree scales (Ehleringer and Cooper, 1988; Gush et al., 2011; McCarthy et al., 2011).

The objective of this research was to study six frequently planted tree species/cultivars, which originate from two contrasting habitats, concerning their potential to reduce urban heat loads. Therefore, we report results obtained from continuous sap flux, monthly stem growth, and crown structure measurements for the summer months in 2016. We aimed to answer the questions (1) whether the native habitat has an effect on the ability to deliver ESS related to water consumption and biomass production and (2) how water use is determined by atmospheric and edaphic conditions as well as crown characteristics.

2. Material and methods

2.1. Study site and species selection

The municipal nursery Munich-Laim (48°08′05″N, 11°28′47″E, 534 m a.s.l.) is located in the Munich Gravel Plain in southern Germany, which comprises sander terraces formed during the Pleistocene as well as by the modern floodplain of the River Isar. Long-term (1981–2010) annual means for temperature and rainfall from the nearest weather station Munich Airport are 8.7 °C and 834 mm, respectively (DWD, 2017). The large 42-ha nursery shows very little variation in terms of microclimatic and edaphic conditions, which is ideal for comparing species-specific physiological and structural traits. Stocking on gravel, the upper soil is 0.5–0.75 m deep and consists of a soil–gravel mixture and a humus layer. With a minimum depth of 10 m below surface level groundwater cannot be reached by the roots.

For the measurement campaign 2016, individuals each of the following deciduous and diffuse porous species/cultivars within the stem circumference size class 16–18 cm were selected: *Acer platanoides* L., *Carpinus betulus* L. 'Fastigiata', and *Tilia cordata* Mill. 'Greenspire' as frequently planted native species/cultivars with presumably less drought tolerance and *Acer campestre* L., *Ostrya carpinifolia* Scop., and *T. tomentosa* Moench 'Brabant' originating from habitats with lower water supply, which appear suitable for future plantings in current street tree trials and scientific field experiments (GALK 2006 & 2012; Fini et al., 2009; Hiemstra, 2011; LWG, 2016) (see Table 1). Because we compared tree species/cultivars from native habitats with higher and lower water availability in a relative sense (Chapin et al., 1993), we hereinafter use the terms high- (HR) and low-resource (LR) species/cultivars. Comparisons were made between both groups as well as, in particular between the two *Acer* species, the *Betulaceae Ostrya carpinifolia* with the native *Carpinus betulus* Fastigiata', and the two *Tilia* cultivars.

The individuals were spread over two separate sites (site A and B) of the nursery at 2 × 3 m spacing. To avoid results being influenced by the phenomenon of transplanting shock (Bühler et al., 2009), individuals that had already been transplanted in spring 2014 were chosen; therefore, the root system architecture should have developed sufficiently in the meantime.

Table 1
Characteristics of the surveyed trees.

	abbreviation	site	DBH [cm ± sd]	crown area [m^2 ± sd]	LAI [$m^2 m^{-2}$ ± sd]
1 commonly planted species/cultivars from species-rich forests and woodlands[1] (HR)					
Acer planatoides	*Ap*	B	5.12 ± 0.10	1.02 ± 0.65	5.80 ± 1.30
Carpinus betulus 'Fastigiata'	*Cb*	A	5.05 ± 0.07	0.49 ± 0.07	6.63 ± 1.65
Tilia cordata 'Greenspire'	*Tc*	A	5.23 ± 0.21	0.55 ± 0.08	4.32 ± 0.93
2 promising species/cultivars from steppes and dry forests[1] (LR)					
Acer campestre	*Ac*	A	4.82 ± 0.14	1.31 ± 0.22	3.92 ± 0.90
Ostrya carpinifolia	*Oc*	B	5.13 ± 0.16	1.43 ± 0.12	4.27 ± 0.74
Tilia tomentosa 'Brabant'	*Tt*	B	5.29 ± 0.16	0.55 ± 0.20	5.18 ± 1.31

[1] according to Kiermeier, 1995; Roloff and Bärtels, 2006.

2.2. Climate variables

Photosynthetically active radiation (μmol $m^{-2} s^{-1}$; PAR) was recorded (LI-190; LI-COR Biosciences, Lincoln, NE, USA) at site B on top of the data logger cupboard in 1-min sampling intervals and averaged to 5-min mean values. Air temperature, relative humidity, wind speed, -direction, and precipitation were sampled every 10 min with a weather station (Davis Vantage Pro2; Davis Instruments, Hayward, CA, USA) placed some 200 m away from the experimental plots. Because of inaccurate readings, precipitation data were also obtained from the nearest weather station at Munich Airport from the German Weather Service (DWD). Vapor pressure deficit (hPa; VPD) as one of the most important environmental drivers for transpiration was computed from 10-min time interval air temperature and humidity data. For response analysis, we also normalized VPD for day length (D_Z) as described in Ewers et al. (2001).

2.3. Soil water measurements

Volumetric soil water content (Vol.-%; VWC) was measured using HS-10 sensors (Decagon Devices, Pullman, WA, USA) inserted horizontally at a depth of 30 cm in the A-horizon and 40 cm away from the tree stems. One or two sensors per species/cultivar were used at one centrally placed individual at the site. In case of two sensors, measurement data were averaged. 5-min means were calculated from 1-min readings and logged (site A: CR800 connected to AM16/32 B multiplexer, Campbell Scientific, Logan, UT, USA; site B: Agilent 34970A Data Acquisition/Switch Unit, Agilent Technologies, Santa Clara, CA, USA).

2.4. Stem growth measurements

From April to October 2016, we measured diameter at breast height (DBH) of each tree at a height of 1 m (nursery workers in Germany measure DBH at 1 m instead of 1.3 m) at the start of each month with a digital caliper. To account for irregularities in the form of the trunks, measurements in two perpendicular directions (N–S, E–W) were performed and averaged.

2.5. Optical measurements of crown structure

For estimations of leaf area index ($m^2 m^{-2}$; LAI), which is the one-sided green leaf area per unit ground surface area, we used the LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences) with a special procedure for measuring isolated plants; the parameter is inferred indirectly from the optical measurements of transmission of radiation (gap fraction) through the canopies. Mean LAI was calculated from the average of one above-crown radiation measurement and four below-crown readings in each sky direction (90° view cap). Because the measured trees were quite small, we used only the two inner rings of the optical sensor (0–28° from the zenith) to ensure that the field of view was within the canopies.

Additionally, we measured a sufficient number of points (8–10 X, Z pairs) on each tree that described its average crown shape. Hemispherical sensor and crown shape data were used to compute LAI and the projected crown area of the study trees with the company software (FV2200). Data acquisition was performed under conditions with uniformly overcast sky in August 2016.

2.6. Stem xylem flux

For whole-tree transpiration measurements we used the thermal dissipation technique with heat as a tracer for sap movement in the stem xylem; all trees were equipped with pairs of 20-mm Granier-type sensors (Granier, 1987): an untreated control and a continuously heated downstream probe (SF-G & CCS, Ecomatik, Dachau, Germany). On the north side of the stems, the sensors were inserted radially into the outer 20 mm of the xylem at or near a height of 1.5 m and 8 cm apart to avoid thermal interference due to heat from the upper heated probe. All sensors were covered with reflective insulation to protect from external temperature and irradiance gradients. Data sampling in June (only site A), July, August, and September took place every minute and 5-min averages were computed and logged in same way as VWC data.

Prior sensor installation, DBH-to-sapwood thickness allometric relationships were obtained by coring (4.3-mm increment corer) one additional tree per species/cultivar of the same circumference-class. Cores were subsequently analyzed for hydro-active xylem using measurements of the visual distinction between lighter colored sapwood and darker colored heartwood. For none of the sample trees the presence of heartwood could be identified. Hence, we assumed no pith and the whole stem as conducting area.

The difference in voltage between the two probes is proportional to the difference in temperature, which decreases as sap flux increases in velocity, because heat is dissipated more rapidly. Granier's empirical equation (1987) was used to convert the voltage values into volumetric sap flux densities (g H_2O cm sapwood^{-2} min^{-1}; J_S):

$$J_s = 0.714\left[\frac{\Delta T_{max} - \Delta T}{\Delta T}\right]^{1.231} \quad (1)$$

with ΔT as the temperature difference between the sensor needles and ΔT_{max} as the maximum temperature difference within a 24-h interval when sap flux is assumed to be zero.

The product of J_S and the cross-sectional sapwood area (cm^2; A_S) at a height of 1.5 m gives an estimate of whole-tree total sap flow (g H_2O min^{-1}; SF).

$$SF = J_s A_s \quad (2)$$

2.7. Crown-level transpiration

To account for variations in crown sizes, we scaled J_S to transpiration per unit crown area (g H_2O m crown area^{-2} min^{-1}; E_C) with sapwood-to-projected-crown area ratio (A_S/A_C) following Peters et al. (2010). A_S was calculated from the trunk diameters at sensor height measured prior to sensor installation; A_C was determined in the course of the LAI approach.

$$E_C = J_s \frac{A_S}{A_C} \quad (3)$$

Variations in leaf amounts were finally taken into account by calculation of transpiration per unit leaf area (g H_2O m leaf area^{-2} min^{-1}; E_L) using the ratio of E_C and LAI:

$$E_L = \frac{E_C}{LAI} \quad (4)$$

2.8. Water-use efficiency (WUE)

As a ratio of some measure of carbon assimilation to some measure of the correspondent water loss, we calculated the water-use efficiency (cm^2 basal-area increment (BAI) kg H_2O^{-1}; WUE) for all sample trees. Carbon assimilation in this case was represented by the amount of stem biomass known from the stem growth measurements.

2.9. Statistical analysis

We tested for significant differences in J_S, SF and crown-level transpiration as well as BAI, crown structure and WUE among the six species/cultivars. First, the data sets were tested for normal distribution (Shapiro-Wilk test). To check for differences in the means of species/cultivars, we then used one-way analysis of variance (ANOVA) for normally distributed data and the Kruskal-Wallis H as the non-

parametric alternative. For additional exploration of the differences among means, we applied post hoc tests (Tukey's post hoc test and Dunn-Bonferroni test); the significance level for all tests was $\alpha = 0.05$.

Additionally, response types and strengths of stem xylem flux to different climatic and edaphic conditions were investigated with the help of regression analyses and correlation tests. Particularly, the relationship between daily J_S and D_Z was analyzed by developing exponential saturation models (Peters et al., 2010) in the form of $y = a(1 - \exp(-bx))$, where a and b are fitting parameters. The models were also used for filling gaps in daily J_S. All statistical analyses were performed using the software package R, version 3.2.2 (R Core Team, 2015).

3. Results

3.1. Environmental conditions

At the phase of leaf development in spring, air temperatures and precipitation amounts reached long-term averages for this time of year. After a quite cold and rainy (88.6 mm) June, July was the warmest month in 2016, with 20.78 °C average daytime temperature and high VPD values (partly > 30 hPa) (Fig. 1). July and August also had the largest precipitation events, which led to the absence of long periods of drought. In September, there was only 62.6 mm of total rain; in particular, the first half of the month was quite warm and sunny including a ten-day period of dryness, still with high VPD values between 10 and 20 hPa and average VWC values close to only 16% at single measurement points (data not shown). Overall, the two sites did not differ significantly in their soil water contents ($P = 0.14$) during the summer. At site A, single measurements points were quite similar to each other, while at site B, there was more variation: at the microsite of *Ap*, there were disproportionately high moisture contents because soil compaction had led to a gentle gradient in the otherwise very even surface area of the nursery. The remaining microsites of *Oc* and *Tt* were up to 10% drier.

3.2. Diurnal course of sap flux density

The observed patterns of diurnal change in the J_S were similar among the six investigated species/cultivars. Shortly before sunrise, stem xylem flux reached a minimum and showed a continuous rising trend towards midday with the increase of light intensity (morning increase; Fig. 2). After a clear peak in the early afternoon, J_S rates declined in the afternoon until they reached very low levels after sunset (evening decline).

Differences between the species/cultivars were highest when J_S values peaked in the early afternoon; averaged over the entire measurement series, the LR species/cultivars peaked with 1.24 times higher daily maximum J_S in comparison to the HR species/cultivars (daily maximum J_S LR: 0.153, HR: 0.189 g H_2O $cm^{-2} min^{-1}$; $P < 0.001$). The difference was also highly significant when both *Acer* species and both *Tilia* cultivars were compared ($P < 0.001$), whereas *Cb* and *Oc* showed no significant difference ($P = 0.679$).

3.3. Impact of species and environmental variables on the dynamics of stem xylem flux

In August, where there was high weather variability, days without rain were characterized by high maximum J_S values, whereas individual days of wet, overcast weather by lower ones (Fig. 2). In reaction to the dry period lasting several days in September with continuously high maximum VPD values (> 20 hPa), there was a tendency for a slight decline in daily maximum J_S values for all species and cultivars except *Cb*. This response, however, was less pronounced for the HR species/cultivars and thus the peaks of the different groups moved ever closer to each other. *Oc* even showed higher maximum J_S values than *Cb* with increasing dryness.

Fig. 3 shows the daily sums of J_S for each species/cultivar in response to D_Z; daily J_S generally showed a saturating response to increasing D_Z. For all LR species/cultivars, average daily sums of J_S were best explained by D_Z in September (R^2 *Ac* = 0.82, R^2 *Oc* = 0.72, R^2 *Tt* = 0.81). The models for *Cb* had the best fits in all months (R^2 July = 0.89, R^2 August = 0.88, R^2 September = 0.86) except June ($R^2 = 0.75$), due to higher variability at low values of D_Z in comparison to *Tc* ($R^2 = 0.88$).

All species/cultivars reached highest asymptotic maxima in June and July, respectively, and showed a continuous decrease with time, as highlighted by the decline of parameter a of the saturation models (Table 2). Monthly sums of J_S decreased as the growing season progressed as well, except for the individuals of *Tc*, which reached highest monthly J_S in July instead of June.

For the entire summer, *Ac* showed the highest monthly sums of J_S, followed by *Tt*, which had in turn slightly higher monthly SF due to the considerably larger diameters ($P = 0.016$) in comparison to *Ac* (Table 1). Except for June, the lowest J_S and SF values were generally found in *Cb*. The individuals of *Oc* had the third highest monthly J_S and

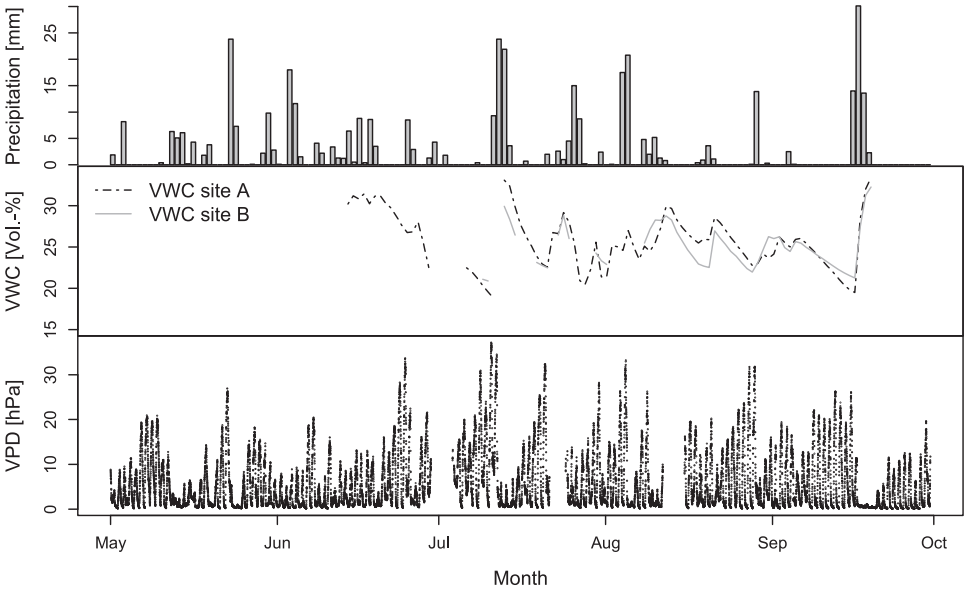

Fig. 1. Daily amounts of precipitation (mm) and mean volumetric soil water content (Vol.-%; VWC) for the two study sites and vapor pressure deficit (hPa; VPD) for the entire study period in 2016. Missing data represent days when the equipment failed. Precipitation data were from the German Weather Service (DWD; available online) measured at Munich Airport.

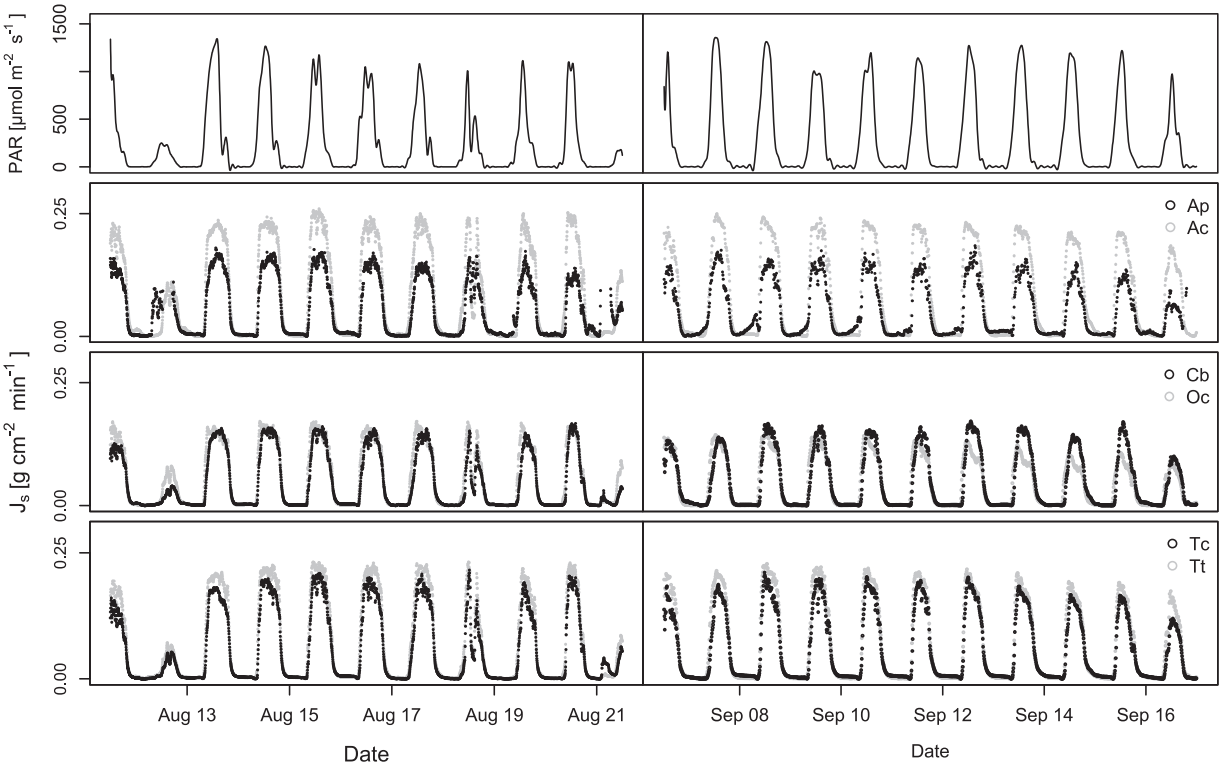

Fig. 2. Patterns of diurnal sap flux density (J_S) and the photosynthetically active radiation (µmol m^{-2} s^{-1}; PAR). Each data point represents the mean J_S values of all trees measured per species/cultivar. For full species/cultivar names, see Table 1.

SF in July, but showed a strong decrease of both parameters in August and September due to more rapid saturation and even single point decrease of J_S at high values of D_Z, indicating greater stomatal regulation (lowered g_S). In August and September, the individuals of *Ac* and *Tt* also showed higher stomatal regulation and faster saturation in comparison to the HR species/cultivars, as is highlighted by the values of parameter b in the saturation models (Table 2).

Among the influencing parameters, the J_S of each species/cultivar

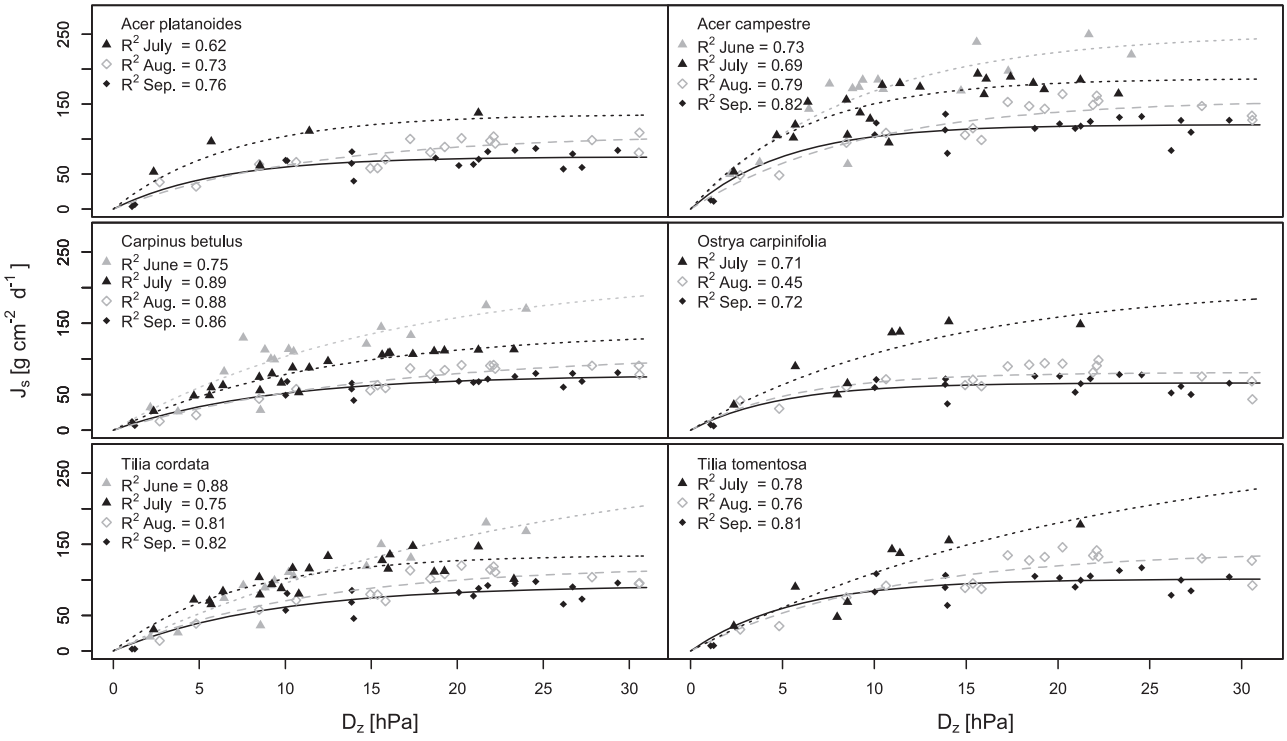

Fig. 3. Daily sums of sap flux density per unit sapwood area (J_S) vs. day length normalized mean daytime vapor pressure deficit (D_Z) for the six species/cultivars in June (only site A), July, August, and September 2016. Each panel represents the mean of all trees measured per species/cultivar. Lines to the data are exponential saturation curves of the form $y = a(1 - \exp(-bx))$.

Table 2
Parameters for the exponential saturation model $J_S = a(1 - \exp(-bD_Z))$ and mean sums of sap flux density per unit sapwood area (l cm^{-2} d^{-1}; J_S) and whole-tree sap flow (l tree^{-1}; SF) for the six species/cultivars in June (only site A), July, August, and September 2016.

species/cultivar	June				July				August				September			
	a	b	J_S	SF	a	b	J_S	SF	a	b	J_S	SF	a	b	J_S	SF
Ap	–	–	–	–	135.61	0.15	3.08	62.8	107.16	0.09	2.32	47.1	74.744	0.16	1.84	37.42
Ac	251.40	0.11	4.37	73.5	186.84	0.16	4.36	73.3	156.49	0.11	3.63	62.4	120.66	0.19	3.09	53.01
Cb	219.18	0.06	2.72	51.7	138.87	0.08	2.41	45.9	108.45	0.07	2.02	38.4	77.32	0.11	1.71	32.47
Oc	–	–	–	–	204.69	0.08	3.46	68.8	80.89	0.18	2.11	42.7	66.40	0.20	1.72	34.68
Tc	285.67	0.04	2.54	47.9	135.39	0.14	2.97	56.4	119.87	0.09	2.55	47.8	92.02	0.11	2.02	37.85
Tt	–	–	–	–	305.00	0.05	3.82	76.7	140.74	0.10	3.12	62.6	101.35	0.18	2.55	51.24

Table 3
Correlation coefficients between different parameters of water use (WU), atmospheric drivers, and edaphic conditions for high- (HR) and low-resource (LR) species/cultivars and to structural crown attributes in general. P-values express the results from comparisons of means between the comparison couples with a significance level of 0.05. N.s. indicates not significant, * statistically significant ($P < 0.05$), ** highly significant ($P < 0.01$), and *** very highly significant ($P < 0.001$).

determinants	atmospheric				edaphic		structural	
WU parameter	D_Z [hPa]		daily PAR [µmol m^{-2} d^{-1}]		max.VWC [Vo.-l%]		crown area [m^2]	LAI [m^2 m^{-2}]
	HR	LR	HR	LR	HR	LR		
daily J_S [g cm^{-2} d^{-1}]	*Ap*: 0.53***	*Ac*: 0.57***	*Ap*: 0.46**	*Ac*: 0.48***	Ap: −0.11n.s.	*Ac*: 0.09 n.s.		
	*Cb: 0.74****	*Oc: 0.31n.s.*	*Cb: 0.54****	*Oc: 0.26 n.s.*	Cb: −0.06 n.s.	*Oc: 0.01 n.s.*		
	*Tc: 0.64****	*Tt: 0.55****	*Tc: 0.48****	*Tt: 0.45****	Tc: −0.18 n.s.	*Tt: −0.15 n.s.*		
total SF [l]							0.66***	
mean E_C [l m^{-2} d^{-1}]								0.53**

was most strongly correlated to D_Z. Furthermore, mean daily sums of J_S generally showed a linear response to PAR with highly significant correlation in *Ac* ($r_S = 0.48$), *Cb* ($r_S = 0.54$), and both *Tilia* cultivars (r_S *Tc* = 0.48 and r_S *Tt* = 0.45), high correlation in *Ap* ($r_S = 0.46$), and no significant correlation in *Oc* ($r_S = 0.26$; Table 3). However, contrary to D_Z, daily J_S did not show saturating response to increasing PAR (data not shown). Daily J_S was not significantly explained by soil moisture for any species/cultivar. Between the amount of transpiration and structural crown attributes, however, there were again strong correlations: high projected crown area led to high sap flow ($r_S = 0.66$) and high LAI was positively associated ($r_S = 0.53$) with E_C.

3.4. Crown and leaf level transpiration

Differences in E_C (Fig. 4) were highly significant in August ($P = 0.009$) and September ($P = 0.003$) between the narrow and pyramidal shaped *Cb* and *Oc*, which had on average the highest projected crown area of all species/cultivars (Table 1). Although not significant, *Ap* and *Tc* also had on average higher E_C values in all three months than their equivalents (*Ac* and *Tt*), with one exception in July, where *Tt* reached higher values than *Tc* due to high daily J_S values and less stomatal regulation than in late summer (see previous subsection and Fig. 3).

In the same way as for E_C, the differences in E_L between the pairs were highest in July and decreased towards the end of summer. In all three months, *Cb* and *Oc* were significantly different. Averaged for all

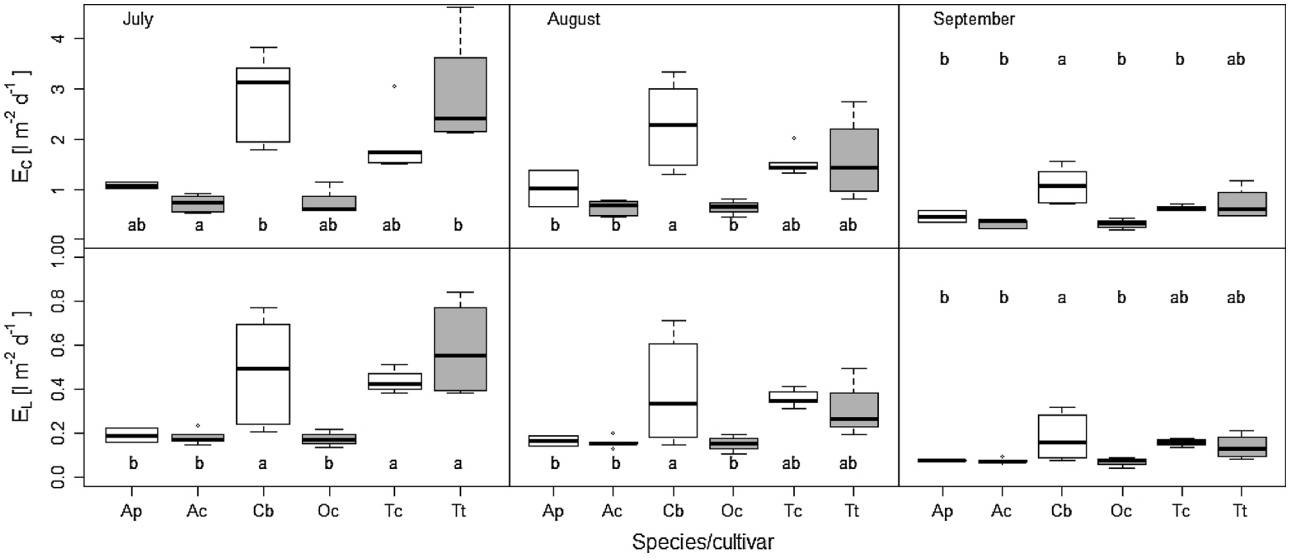

Fig. 4. Side-by-side comparison concerning the average transpiration per m^2 crown area (E_C) and the average transpiration sum per m^2 leaf area (E_L) of the high- (white) and low-resource species/cultivars (gray boxes) in July, August, and September 2016. Different letters indicate statistically significant differences between the species/cultivars at $\alpha = 0.05$.

three months and scaled to the smallest level (E_L; l m^{-2} d^{-1}), water use of the species/cultivars was as follows: *Cb* (0.352) > *Tt* (0.344; far highest transpiration rate of the LR species/cultivars) > *Tc* (0.339) > *Ap* (0.147) > *Ac* (0.141) > *Oc* (0.134 l m^{-2} d^{-1}).

3.5. Growth and efficiencies of water use

The highest and most consistently year-round growth rate was exhibited by *Tt*, with an average of 9.1 cm^2. *Oc* had the second highest growth (6.83 cm^2), which was significantly different from those of *Tc* (5.16 cm^2), *Ac* (4.94 cm^2), *Ap* (4.2 cm^2), and *Cb* (3.49 cm^2). The LR species/cultivars exhibited much more vigorous growth in comparison to the HR species/cultivars ($P < 0.001$). Total BAI of *Tt* was significantly higher ($P < 0.001$) than of *Tc*; the individuals of *Oc* also exhibited significantly higher growth than *Cb* ($P = 0.002$), whereas the two *Acer* species were more similar ($P = 0.94$).

Moreover, in the period from July to September, for which growth and water use data are available for all six species/cultivars, different trends in growth and transpiration explained differences in WUE. Averaged for all three months, the highest WUEs were observed in the three LR species/cultivars *Tt* (2.55 ± 0.5), *Oc* (2.32 ± 0.39), and *Ac* (1.75 ± 0.66 cm^2 BAI/100 l H_2O), followed by the HR species/cultivars *Tc* (1.66 ± 0.58), *Cb* (1.64 ± 0.47), and *Ap* with only 1.30 ± 0.87 cm^2 BAI/100 l H_2O (data not shown).

In July, there were no significant differences in WUE among the species/cultivars. In this month with high water availability (Fig. 1), all HR species/cultivars as well as the individuals of *Ac* showed their most efficient use of water. Later in summer, however, *Oc* and *Tt* had higher WUE (Fig. 5).

In August, the individuals of *Tt* had the highest WUE of all species/cultivars as a result of high water use on the one hand but even higher growth on the other (Fig. 6); their average BAI of 2.17 cm^2 was almost five times the BAI of *Tc* (0.44 cm^2) and seven times the BAI of *Cb* (0.31 cm^2), but the transpiration amounts were only less than twice as high (SF *Tt* = 63.24 l, SF *Tc* = 49.25 l, SF *Cb* = 37.16 l). The low WUE in July, however, was a result of both relatively high BAI and transpiration; the individuals of that cultivar had on average almost three times the BAI of *Ap* (2.49 cm^2 and 0.92 cm^2) and more than 2.5 times the transpiration of *Cb* (118.77 l and 45.11 l). WUE of *Oc* was also low in July; in this case, however, it was due to both low BAI (1.15 cm^2) and transpiration (52.44 l). Moderate to high BAI (1.06 cm^2 and 1.16 cm^2) combined with low transpiration (46.17 l and 20.82 l) led to a high WUE in August and even the highest WUE of all species/cultivars in September. *Ac* had the highest WUE of all LR species/cultivars in July due to high BAI (1.64 cm^2) and transpiration (69.61 l), but showed a considerable decrease in WUE in August and September mainly due to very high transpiration at moderate BAI.

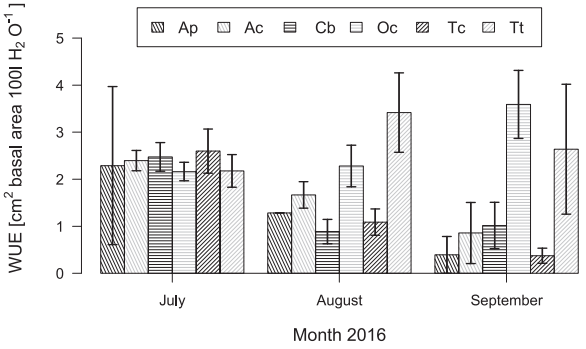

Fig. 5. Side-by-side comparison of the water-use efficiencies (WUE) in July, August, and September 2016 for all species/cultivars, presented as basal-area increment (BAI)/transpiration. White bars are high- and gray bars are low-resource species/cultivars. Data are means ± sd. Different letters indicate statistically significant differences between the species/cultivars at $\alpha = 0.05$.

Of the HR species/cultivars, the individuals of *Cb* showed the lowest transpiration in each month (July: 37.16 l, August: 45.1 1, September: 37.16 l) and moderate (July: 1.14 cm^2, September: 0.20 cm^2) to very low (August: 0.31 cm^2) BAI, leading to moderate (July and August) to very low (September) WUE. *Ap* achieved low WUE mainly because of very low BAI in July and September (0.92 and 0.06 cm^2) combined with moderate transpiration amounts (60.40 l and 23.04 l), and in *Tc* low BAI (0.44 and 0.08 cm^2) and moderate transpiration (49.25 and 20.86 l) were observed in August and September leading to low WUE in these months as well.

4. Discussion

In this study, we attempted to derive the potential of six different urban roadside tree species and cultivars, to reduce urban heat loads, which are assumed to vary in their drought tolerance because they originate from two contrasting habitats. The data show that the investigated species/cultivars differed in their magnitude and seasonality of stem xylem flux, crown-level transpiration, WUE, growth, and crown structural attributes.

4.1. Species differences in stem xylem flux in response to environmental variables

Strong linear correlations of J_S with PAR and the sigmoid-shaped response to D_Z showed that those are the key environmental variables for explaining plants' water use, as also found in other studies (Ewers et al., 2001; Peters et al., 2010; Gillner et al., 2015a). Even though low soil water availability is expected to lead to reductions in stem xylem flux, we did not find any significant correlations. Therefore, VWC does not appear to be an important control on stem xylem flux, at least under conditions of sufficient water availability, such as that in summer 2016. Other studies also did not find significant correlations (Peters et al., 2010; Gillner et al., 2015a), whereas in the drought year 2015, Rahman et al. (2017) measured lower transpiration rates for *Tilia cordata* under harsh conditions with soil moisture potential below −1.5 MPa.

Generally high J_S values of the LR species/cultivars and their particularly high capacity for transpiration in early summer are consistent with observations from other researchers, where LR species also did not show lower J_S in comparison to HR species (McCarthy et al., 2011; Goedhart and Pataki, 2012). Gebauer and Ehleringer (2000) found the capacity for transpiration to be highest following infrequent and unpredictable precipitation events, as it was also apparent in July 2016 with unusually large amounts of rain within short periods (Fig. 1). As the growing season progressed and the longest dry period occurred in September, however, the LR species/cultivars showed a tendency to exhibit increased and earlier regulation of water use with high D_Z, indicating higher stomatal sensitivity to VPD. A study of Fini et al. (2009), investigating irrigation effects on growth and physiology of different *Tilia* species and *Ap* cultivars during the establishment phase, found leaf gas exchange of *Tc*, *T.* x *europaea* and two out of three *Ap* cultivars only little affected by water shortage (water spending strategy), whereas *Tt* showed high gas exchange only under irrigated conditions but reduced g_S and transpiration in the drought treatment (drought avoidance). Low stomatal regulation under increasing VPD for *Ap* was also found in the study by Gillner et al. (2015a). Under heat and drought, however, Bush et al. (2008) found low g_S of *Ap*; in addition, in the study by Forrai et al. (2012), *Acer* was the genus exhibiting lowest g_S around midday in comparison to *Tilia* and *Fraxinus* species. One explanation for this proposed by Gillner et al. (2015a) was the sufficient soil water the trees were exposed in their study. Because of the instable weather 2016 and in particular the disproportionately high soil moisture content at the microsite of *Ap*, we also did not assume our trees had experienced severe drought stress at any time.

In the relative comparison between H- and LR species/cultivars, our results are in line with the view that species originating from habitats

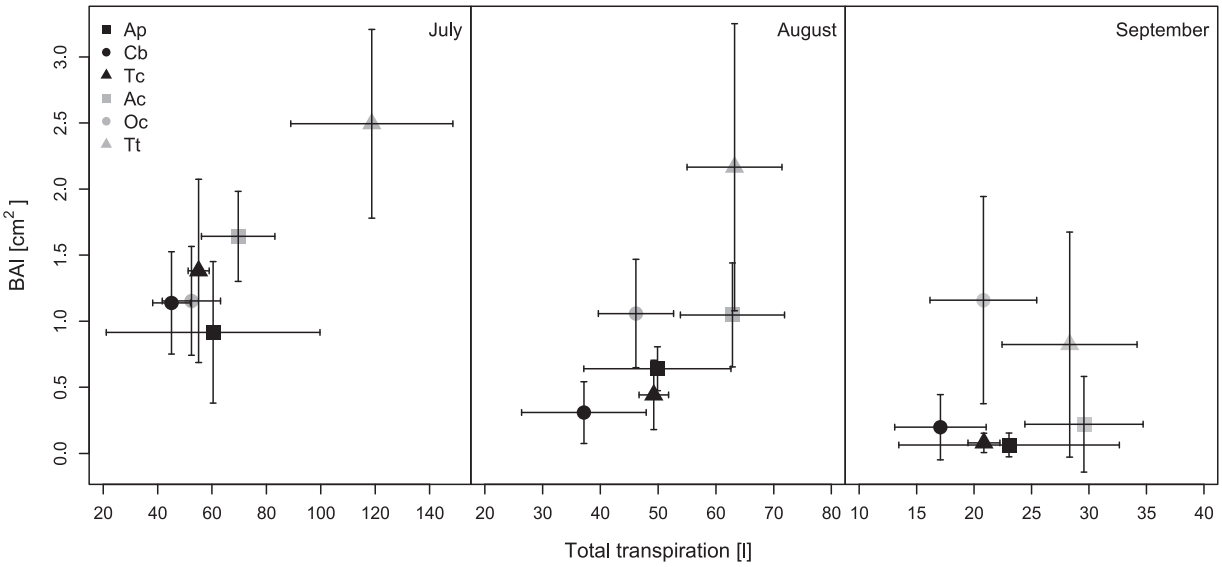

Fig. 6. Basal-area increment (BAI) vs. total transpiration in July, August, and September 2016. Black symbols are the high- and gray symbols the low-resource species/cultivars. Data are means of all trees measured per species/cultivar ± sd. Note the different horizontal axes for the three months.

with high water supply show a lack of efficient prevention strategies to avoid tissue water deficits, what can make them less resistant in times of long-lasting droughts (Lösch, 2003). However, the higher flexibility in water use that we have seen for the LR species/cultivars is helpful to get through drought periods without major damage on the one hand (Lösch, 2003), but also to compensate those periods with high capacity for transpiration (Gebauer and Ehleringer, 2000) in times of high resource supply on the other.

4.2. Crown- and leaf-level transpiration

It has become evident that data of the crown structure can be seen as another important indicator for properly assess the magnitude of ESS related to water loss. Even though all investigated species/cultivars were in the same circumference class, crown dimensions and leaf area were not uniform among them; at the juvenile stage, the cultivar *Tc* 'Greenspire' is known to have a light, irregular crown, while *Tt* 'Brabant' has broadly conical and thickly covered crowns. *Cb* 'Fastigiata' has narrow pyramidal and dense crowns in comparison to the broad and ovate growing *Oc* (LWG, 2016) with on average lower LAI.

Transpiration and the associated benefit of transpirational cooling are directly linked to the amount of (healthy) leaf surface area (Lösch, 2003; Peters et al., 2010; Gillner et al., 2015a). Heat-based xylem flux methods, typically used at stem level however do not take into account those differences in crown sizes and structure. Species differences in water use, however, can only be derived by means of scaling. After applying this method, the LR species/cultivars did not solely have higher rates of water use. Contrarily, throughout August and September, prevention strategies to avoid tissue water deficits led to lower transpiration rates in comparison to those in their respective HR-equivalents.

Within the HR species/cultivars, *Ap* had lowest E_C and E_L values in all months. Gas exchange measurements at urban sites in Dresden, eastern Germany (Gillner et al., 2015a), also indicated lowest g_S and transpiration for adult *Ap* among five investigated tree species. Forrai et al. (2012) came to similar results when comparing a cultivar of *Ap* with other species and cultivars of *Tilia* and *Fraxinus* in late summer in the Arboretum of Budapest, Hungary. In their study, *Tc* exhibited highest rates of g_S and transpiration, followed by *Tt* and the cultivars *Tt* 'VI' and *Tt* 'Balaton'. For September, our findings correspond with these results; for the whole summer however, the individuals of *Tt* had slightly higher E_L values than *Tc* due to their very high water consumption in July.

4.3. WUE and growth

Gush et al. (2011) assumed that the growth rate of plants is linked to WUE, as was also the case in our experiment: the LR species/cultivars had on average higher WUE during summer with increasing differences as the year progressed. The same as for transpiration, *Ap* had lowest WUE of all six species/cultivars because of very low growth and water use, corresponding again with the results of Gillner et al. (2015a). In addition, Forrai et al. (2012) found leaves of both *Tc* and *Tt* (pure species and two cultivars) to have higher photosynthetic capacity and transpiration rates in comparison to the cultivar *Ap* 'Crimson King'. Within the genus *Tilia,* WUE was highest for the cultivar *Tt* 'VI' followed by *Tc* and *Tt*.

More efficient use of water by species originating from areas with low water availability in comparison to HR species has already been found in several other studies (e.g., Ehleringer and Cooper, 1988; Gush et al., 2011; McCarthy et al., 2011). In this context, McCarthy et al. (2011) found VPD in the native habitats to be a suitable predictor of species WUE. In the case of the three LR species/cultivars, their high WUE was not associated with low growth, except in the case of *Oc* in July; for *Oc* and *Tt* it was mostly high growth and relatively low transpiration rates that led to high WUE; for *Ac*, in turn, it was both, high growth and high transpiration rates. Because of the instable weather conditions in 2016, however, we could not observe patterns in whole-tree WUE under severe drought conditions. The temporal resolution of the stem increment measurements was too low to account, for instance, for the dry first half of September but disregard the rainy period in the middle of the month (Fig. 1). Future studies should therefore include high-resolution growth observations with electronic dendrometers, which yield more precise information not only about diameter growth, but also about diurnal variations in trees water use.

4.4. Conclusions – urban roadside trees for a warmer future

For future plantings, species and cultivars that are adapted to the changing urban climate and tolerant to various stressors are of interest (Bühler et al., 2009). For this purpose, LR species/cultivars can reasonably be considered promising for future tree plantings because they provide a good balance between water loss and growth; they also show

mechanisms, which make them being less dependent on the environment for new resources (Chapin et al., 1993). Since transpiration is positively correlated to g_S (Forrai et al., 2012), however, planting LR species/cultivars may lead to reductions in transpirational cooling. Despite a higher cooling ability at the leaf level, however, we expect trees with a water-spending strategy to prove unsustainable in times of severe drought, because they are supposed to show earlier onset of wilting, leaf abscission (in extreme cases up to death) and therefore, nothing is gained in terms of climate regulating ESS. In our study, the water use of species/cultivars was determined by both the environmental conditions and the leaf amounts of the trees. For high cooling effects, we therefore suggest planting LR species/cultivars, which are known to develop densely leaved and voluminous crowns to compensate their lower water use when dryness occurs. Among the three promising LR species/cultivars, *Tt* is assumed to provide the most substantial cooling effect because of its dense foliage and large diameter. Under favorable conditions and scaled to leaf level, *Tt* can transpire the same (Fini et al., 2009) or even more water than *Tc*. Smaller benefits can be estimated for *Ac*, the water use of which is limited mainly due its thin stems and low LAI. Despite this, its water use is still higher than that of *Ap*. *Oc* appeared to be most sensitive to dryness and to have a low LAI as well, resulting in lowest water use of all LR species/cultivars but quite similar to *Cb* because its transpiring leaf surface was also low due to very narrow growth (LWG, 2016).

Since 2016 was not a dry year, the artificial induction of drought in future experiments might provide more information about the behavior of species/cultivars, and in particular the stomatal regulation when they experience long-lasting drought. Because we had almost no spatial heterogeneity in the nursery, we assume that these results reflect mainly genetic and physiological differences in the investigated species/cultivars. High reproducibility means also, however, that the results of this study are not fully transferable to the specific growth conditions at the roadsides, which are known to influence the magnitude and seasonality of the microclimatic benefits of trees (Ferrini and Baietto, 2006; Armson, 2012; Rahman et al., 2017). Furthermore, the situation in the nursery, where trees are planted in rows fully exposed to the sun, may limit the comparability of our data with measurements made in forests. We need more research for understanding the differences in ESS between species and cultivars originating from contrasting habitats. Profound knowledge can lead to a strategic enhancement of the genetic diversity of inner city plant stocks that will constitute real progress not only towards climate change adaptation, but also towards resistance to diseases, pests, and other adverse environmental features.

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